CHAPTER 5

EFFECT OF *COROPHIUM VOLUTATOR* ON THE ERODABILITY OF COHESIVE INTERTIDAL SEDIMENTS

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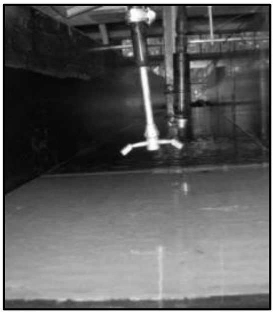
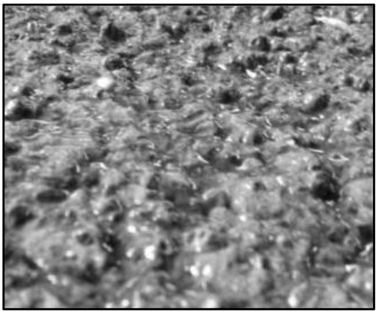

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CHAPTER 5

EFFECT OF *COROPHIUM VOLUTATOR* ON ERODABILITY OF COHESIVE INTERTIDAL SEDIMENTS

ABSTRACT

Despite the importance of mudflats as natural sea defenses and wildlife habitats, the effects of various biota on cohesive sediment erosion are poorly understood. In this study, the influence of Corophium volutator on sediment bed erodability, expressed in terms of suspension erosion rate, critical flow velocity and critical shear stress for erosion, was investigated in a laboratory flume on cohesive sediment from a mudflat without and with different densities (4,000 – 20,000 ind./m²) of Corophium volutator. Suspension erosion rate at the onset of erosion was determined with an Optical Backscatter Sensor, and critical shear stress for erosion was derived from turbulence measurements using an Acoustic Doppler Velocimeter. A significant exponential increase in suspension erosion rate with density was found, where sediment with 20,000 ind./m² showed a five times higher erosion rate than sediment without Corophium. On the other hand, critical shear stress was found to be independent of Corophium density, at least for densities up to 15,000 ind./m². At 20,000 ind./m², a large decrease (-30%) in critical shear stress was measured. Comparison between critical flow velocities obtained in this experiment and hydrodynamically simulated flow velocities over the mudflats where Corophium was collected indicates that bed erosion is unlikely to happen under natural flow conditions, but it might occur under storm conditions.

KEY WORDS: bioturbation, *Corophium volutator*, erosion rate, flume experiment, intertidal sediments

1. INTRODUCTION

The influence of biota on topography and landscapes is still largely unexplored (Gabet *et al.*, 2003; Dietrich and Perron, 2006). Erosion laws that explicitly include biotic effects are needed to explore how intrinsically small-scale biotic processes can influence the form of entire landscapes. To include biotic effects into erosion laws, these small-scale biotic processes need to be understood (Borcard *et al.*, 2004; Dietrich and Perron, 2006), e.g. explaining the self-organisation processes which are often seen in ecosystems requires knowledge on the small-scale biotic processes (van de Koppel *et al.*, 2005; van der Wal *et al.*, 2008b), and models including spatially explicit bio-physical interactions and scale-dependent processes (Borcard *et al.*, 2004).

The erodability of cohesive intertidal sediments is influenced by physicochemical sediment factors and biological factors (Berlamont *et al.*, 1993; de Brouwer *et al.*, 2000; Paterson *et al.*, 2000; Andersen, 2001; Amos *et al.*, 2004). Important physicochemical factors, which influence the erosion, but also the transport, deposition and consolidation of the surface sediment, are the water content, bulk density, grain size distribution and the mineralogy of the sediment particles (Dyer, 1986; Mitchener and Torfs, 1996; Winterwerp and van Kesteren, 2004; Yang, 2003). Physicochemical factors of cohesive sediments have been correlated with surface sediment stability for some time (Hayter and Mehta, 1986; Black, 1997; Dade *et al.*, 1992; Mitchener and Torfs, 1996; Winterwerp and van Kesteren, 2004), whilst it is only recently that biota have been included in the prediction of surface sediment stability (Paterson *et al.*, 2000; Paarlberg *et al.*, 2005). The biotic components can either hamper or enhance erosion, meaning that the consequences for sediment transport are either stabilisation or destabilisation (Willows *et al.*, 1998; Grant and Daborn, 1994; de Brouwer *et al.*, 2000; Widdows and Brinsley, 2002). Microphytobenthos has a stabilising effect through secreting extracellular polymeric substances (EPS), which stick sand grains together and form a protective biofilm (Yallop *et al.*, 1994; de Brouwer *et al.*, 2005; Le Hir *et al.*, 2007). Macrobenthos (bottom living animals > 1 mm) may influence the sediment and its dynamics in several ways: (1) by increasing the bottom roughness and/or making it more heterogeneous, (2) by inducing particulate fluxes, and (3) by changing the sediment erodability through bioturbation or stabilising processes (Le Hir *et al.*, 2007). The influence of macrobenthos on sediment behaviour is complex due to the diversity of the macrobenthos with different life modes for different species, and the fact that even for a single species, opposite effects can exist (Jumars and Nowell, 1984a).

For the mud shrimp, *Corophium volutator* (Crustacea, Amphipoda), some controversy exists about the (de)stabilising effect, since contradictory results have been reported (Grant and Daborn, 1994; de Deckere *et al.*, 2003), depending upon the age of the animals, density of the burrows and the sediment grain size (Le Hir *et al.*, 2007). *Corophium* is an abundant deposit and/or filter feeding species in intertidal mudflats. Population densities frequently reach > 20,000 ind./m^2, and in summer months densities can locally exceed 100,000 ind./m^2 (Gerdol and Hughes, 1994a). The high population densities make this amphipod an important species in many mudflat ecosystems, where it is a significant prey for migratory shorebirds and juvenile flounders (Boates *et al.*, 1995; Murdoch *et al.*, 1986). It lives in U shaped burrows in the upper 5 cm of the sediment (Meadows and Reid, 1966), and the burrow walls are strengthened with a mucus secretion (Meadows *et al.*, 1990). This reduces the erodability of the sediment (Grant and Daborn, 1994; Meadows and Tait, 1989), and may result in an elevation of the seabed (Mouritsen *et al.*, 1998). On the other hand, the U shaped tubes can protrude 1 to 1.5 mm above the sediment surface, and thereby increase sediment roughness (Meadows and Reid, 1966), which increases erosion rate (de Deckere *et al.*, 2003). Eckman and Nowell (1984) suggested that the protruding burrows enhance the microturbulence, resulting in scour around the burrow causing destabilisation. However, high densities of protruding structures can also hamper local hydrodynamics, and protect the sediment from erosion by increasing the height of the benthic boundary layer or even by replacing it to a higher position in the water column (cf. skimming flow by Friedrichs *et al.*, 2000). Furthermore, sediment erodability was observed to increase indirectly by grazing on the biofilm (Gerdol and Hughes, 1994a; Grant and Daborn, 1994; Hagerthey *et al.*, 2002), and directly through an increase in erosion rate caused by resuspension of fine sediment due to feeding and burrowing (de Deckere *et al.*, 2000). In addition, the resuspension of fine sediment can reduce biofilm biomass by inhibiting photosynthesis due to an increased turbidity (Dyson *et al.*, 2007).

Due to bioturbation of the top few centimeters, a mucus- and biodeposit-rich surface layer (often called the "fluffy" layer) is formed. Resuspension of these flocs and recently deposited material, not incorporated into the bed, occurs at low flow velocities and is termed type Ia erosion (Amos *et al.*, 1992; Orvain *et al.*, 2006; Widdows *et al.*, 2009). Widdows *et al.* (2009) found small influences of biota densities on the onset of type 1a erosion, and considered these critical velocities as not of great environmental significance. Erosion of the actual bed layer occurs at higher shear stresses, when large layers of sediment are eroded and mobilised. Bed erosion can be time dependent, i.e. exponential decrease of sediment release with time at constant flows (type Ib), or constant with time with a continuous release of sediment to the water column (type II) (Amos *et al.* 1992).

In this study, the main objective was to investigate the influence of *Corophium volutator* density on major bed erosion. For that reason, a flume experiment was set-up in which only one parameter i.e. density, varied between the treatments. We chose not to include a diatom biofilm, since this could be a confounding factor interfering with the interpretation of the density-erodability relationship, considering that biofilm biomass would probably be affected differently over time between the different density treatments.

2. Material and methods

2.1. Erosion flume and its instruments

The flume in the Hydraulic Laboratory of the K.U.Leuven is a straight flume of about 9 m long, 40 cm wide and 40 cm deep with a closed recirculating water system (Fig. 1). The water used in the flume is fresh water (0 psu), because of environmental constraints when discharging the water after the experiments in the Dijle river. The first 4 m of the flume is the inflow region with a rigid, wooden false bottom of 8 cm high to provide a fully developed turbulent flow in the test section. The test section is 2.9 m long but had to be shortened with a wooden false bottom to 40 cm for this experiment, because with the large section of 1.16 m^2, it was logistically impossible to collect enough animals to reach appropriate densities. The test section has glass walls on one side facilitating visual inspection of the sediment bed and the erosion processes. Downstream of the test section, a sediment trap was constructed with a length of 0.6 m to measure the bed load. The last part of the flume is the outflow section of 1.5 m long which prevents the flow from being disturbed by the sediment trap. A tail gate at the end of the flume can be used to regulate water levels, which varied between 14.3 and 20.5 cm.

The discharge through the flume was measured continuously with a calibrated Kent-Veriflux electromagnetic flow-meter (EMF). Velocities and turbulence were measured in three dimensions and at high frequencies (25 Hz) with a 16 MHz microADV (Acoustic Doppler Velocimeter) from Sontek. This instrument measures velocities in a cylinder of water with a diameter of 4.5 mm and a height of 5.6 mm at 5 cm from the instrument's transmitter and receivers. The turbidity was measured every second with an Optical Backscatter Sensor (OBS) at a distance of 3.5 cm from the bottom. The instrument was calibrated to relate the amount of scattering to the suspended sediment concentration (SSC).

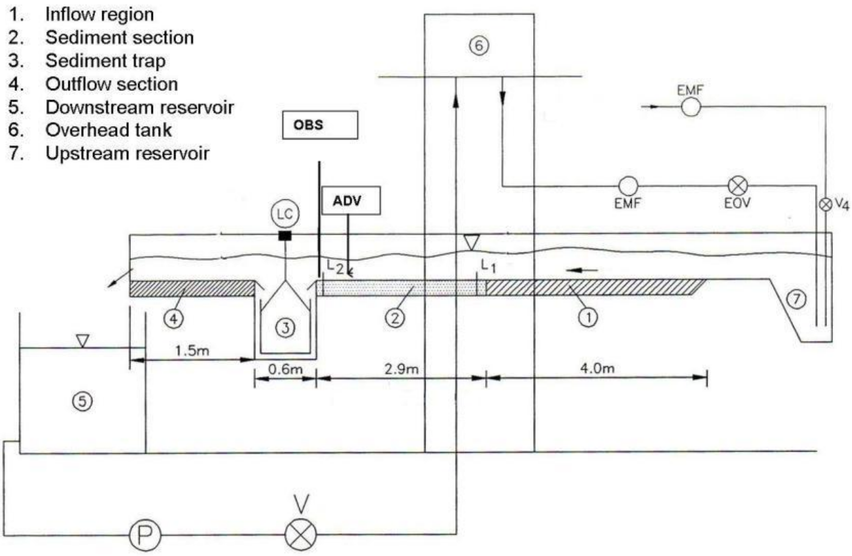

Figure 1: Side view of the rectangular flume.

2.2. *Corophium volutator* and sediment

Sediment and *C. volutator* were collected in June 2008 in the Flemish nature reserve "IJzermonding", a mudflat-saltmarsh area in Nieuwpoort (Belgium, 51°08'N, 2°44'E). The sediment was defaunated by three cycles of 24h freezing – 24h thawing. Grain size analysis (Malvern Mastersizer 2000 laser diffraction) showed that freezing-thawing did not alter median grain size (t-test, $p=0.48$). To reduce natural heterogeneity and to obtain equal starting conditions, the sediment was homogenised by thorough mixing and saturation with seawater before use. The sediment had an average median grain size of 140.6±SD 2 μm, and the following distribution over the different fractions: 7.6% was smaller than 4 μm, 25.1% between 4-38 μm and 4% between 38-63 μm, 9% between 63-125 μm, 33.8% between 125-250 μm, 20.3% between 250-500 μm and 0.04% between 500-800 μm. Eight sediment mesocosms were established by transferring the homogenised sediment into wooden boxes with the size of the test section (L:40 cm x W:40 cm x H:8 cm). Each box was filled completely with sediment, and gently submersed (without disturbing the sediment surface) in separate plastic aquaria for three days to allow the sediment to consolidate. All aquaria were placed in a temperature controlled climate room (16 ± 1° C) with a 12:12h light:dark regime.

After consolidation of the sediment, *C. volutator* was added to the sediment mesocosms in different densities. A density series of 0 (2x); 4,000; 6,000; 8,000; 10,000; 15,000 and 20,000 ind./m^2 was set up, leading to eight erosion experiments in total (2 references and 6 with *Corophium*). The density treatments were not replicated due to logistic and time constraints. The length and the sex of the experimental *Corophium* population was determined for 100 individuals: 69% females (9.2±0.3 mm), 16% males (9.4±0.3 mm) and 15% juveniles (1.6±0.01 mm). After the addition of *Corophium*, the aquaria were subjected to a simulated tidal regime, resembling the natural tidal conditions (i.e. 3h submersion and 9h emersion). Mortality in the mesocosm was very low and never exceeded 1.25%. After 6 days of biological activity, the mesocosms were put one by one, and ad random in the test section of the erosion flume before the start of the erosion experiment.

2.3. Erosion experiment

Sediment erodability is expressed in terms of critical shear stress for erosion, representing the interaction between the flowing water and the sediment bed at the onset of erosion, and the erosion rate, a measure of the amount of material eroded during time (Graf, 1971). During the erosion experiments, the average flow velocity, calculated as:

$$\overline{U} = \frac{Q}{WH}$$

with Q is the discharge, W is the width of the flume and H is the water level. Discharge in the flume was stepwise increased until erosion occurred, while flow parameters and suspended sediment concentration were measured. Stepwise increase in flow velocity was not constant between treatments, as a manual discharge regulator was used with which it was impossible to obtain constant discharge intervals.

2.4. Shear stress determination

Bed shear stress (for short 'shear stress' in this paper) was estimated from turbulence measured by an ADV (Song and Chiew, 2001; Biron *et al.*, 2004; Pope *et al.*, 2006; Andersen *et al.*, 2007). These single point measurements of turbulence should be acquired at the elevation of maximum Reynolds stresses. Based on low-Reynolds boundary layer theory and data, the peak stress can be estimated to occur at ±3% of the water depth (± 0.6 cm for a water level of 18 cm). However, it is practically not possible to position the ADV at such a distance of the sediment surface, because 1) the sampling volume of the ADV has a vertical dimension of 0.56 cm, 2) the sediment surface is not completely smooth, and 3) due to erosion the distance to the bed surface will change, hereby possibly positioning the sampling volume within the sediment. Therefore, the ADV sampling volume was placed at a distance of 1.5 cm from the sediment bed, which is equal to 7 to 10% of the water levels. In an experimental study in a similar laboratory flume, Biron *et al.* (2004) suggested undertaking single-point measurements at 10% of the water level, corresponding to the experimentally determined peak value height in profiles of Reynolds and TKE shear stress. The velocities should be measured for three minutes at 25 Hz to acquire enough samples for these methods based on second order statistics (Adam, 2009).

Shear stress was derived from the turbulent kinetic energy (TKE) as:

$$\tau_{TKE} = C_1\left[0.5\rho\left(\langle u'^2\rangle + \langle v'^2\rangle + \langle w'^2\rangle\right)\right]$$

where u', v' and w' are the velocity fluctuations in the stream wise, lateral and vertical directions respectively, $< >$ denotes an average and C_1 is an empirically derived coefficient and equal to 0.19 (Huntley, 1988; Soulsby, 1983).

The critical flow velocity and shear stress were assumed to correspond to the flow velocity or local bed shear stress at the onset of a continuous increase in suspended sediment concentration measured by the OBS.

2.5. Erosion rate determination

The erosion flux is defined as the mass of sediment eroded per unit of time and per unit of area (kg/m^2s). It consists of bed load and suspended sediment.

The bed load could not be determined, because the load cell of the sediment trap was not sensitive enough for the small weights of the trapped sediment.

The rate of suspension is defined as the mass of sediment suspended per unit of time and per unit of area (kg/m^2s):

$$E_s = \frac{dC}{dt}H$$

where C is the depth-averaged suspended sediment concentration (SSC) and H is the average water depth. In practice, the change in SSC (= dC) was calculated as the difference between the averaged SSC (average of all OBS loggings at a discharge step) at discharge step *i+1* and the averaged SSC at discharge step *i*, where erosion starts at step *i*. In this formula, it was assumed that the water column was well mixed so that the suspended sediment concentration measured by the OBS at one water depth i.e. 3.5 cm, could be used as estimator of *C*. A SSC profile would increase the accuracy of E_s estimates considerably, but this was not available. Therefore, estimates of E_s should be considered qualitatively.

2.6. Statistical analyses

Simple linear models (lm) were applied in the statistical environment R (www.r-project.org) to test for relations between density and average critical flow velocity, critical shear stress and suspension erosion rate. The assumptions of linearity, homoscedasticity and independence of the errors were verified graphically. Normality of the residuals was confirmed numerically with a Shapiro Wilks test. Suspension erosion rate was square root transformed to meet the assumptions. Although, Cook's distance revealed that the density treatment of 20,000 ind./m^2 was an influential data point for erosion rate, it was biologically relevant and important to keep this treatment in the analyses. For critical shear stress, the normality and linearity assumptions were violated, no data transformation was appropriate, but addition of a quadratic term allowed to meet the assumptions. To test if density affected the relationship between suspended sediment concentration and average flow velocity after the onset of erosion, analysis of covariance was conducted to compare slopes of the regressions. Therefore, SSC values were dimished with SSC at the start of erosion to allow for comparison between the different treatments. To meet the assumption of linearity, average flow velocity was squared.

3. Results

3.1. Visual observations

At the highest density of *Corophium volutator* (20,000 ind./m^2), burrows were evenly distributed and covered the entire sediment surface (Fig. 1e), while for the lower densities, patchiness in burrow densities was observed (Fig. 1c). The sediment surface with *Corophium* burrows was heterogeneous, and with a more muddy and humid appearance compared to control treatments (Fig. 1). The turbidity of the water in the aquaria with *Corophium* increased at each flooding event. Even though the water velocity was almost 0, material was resuspended due to active resuspension of the animals flushing their burrows to remove accumulated faeces and excess sand grains (De Backer *et al.*, 2010). At the onset of the erosion experiments, active resuspension was observed as plumes of sediment flushed out the burrows. At higher velocities ($\bar{U}$=0.2-0.25 m/s), the sediment between the burrows eroded, leaving a smooth surface with protruding burrows. After further increase of the current velocity ($\bar{U}$) up to 0.35-0.5 m/s dependent on the treatment, a ridge appeared around the burrows, which eroded further till grooves were formed (Fig. 1d and f). This indicated the start of continuous erosion. For all *Corophium* treatments, local erosion around the burrows was observed, also for the low density treatmens (Fig. 1d).

3.2. Erodability measurements

Figures 3a and b show the critical average flow velocity and critical shear stress in relation to *Corophium* density. No significant regressions were found between critical average flow velocity or critical shear stress and density (Table 1), indicating that (lower) densities of *C. volutator* did not influence critical flow velocity or critical shear stress compared to the control sediment. However, for the density treatment of 20,000 ind./m^2, a large decrease in critical average flow velocity and critical shear stress was measured, on average respectively -25% and -30% compared to the sediment with no or less *Corophium* (Fig. 3).

For the initial suspension erosion rate (Fig. 3c), a significant (p=0.035) linear increase was found with density (Table 1). The significant relationship was influenced by the highest density of 20,000 ind./m^2, where the erosion rate of 0.0022 g/m^{2}s was five times higher than for the sediment without *Corophium* at the onset of erosion (Fig. 3c).

Table 1: Results of simple linear (polynomial) regression models to test for significance of *Corophium* density on critical average flow velocity (U_{crit}), critical shear stress (τ_{crit}) and suspension erosion rate. Significant p-levels are bold.

Variable	Predictor	Coefficient (SE)	p-value	Regression	
				p-value	R^2 adj
τ_{crit}	Intercept	0.16 (0.014)	0.0007	0.19	0.28
	Density	$4.7*10^{-6}$ ($3.4*10^{-6}$)	0.24		
	Density²	$-3.1*10^{-10}$ ($1.7*10^{-6}$)	0.13		
U_{crit}	Intercept	47.1 (2.7)	<0.0001	0.13	0.23
	Density	$-4.6*10^{-4}$ ($2.6*10^{-4}$)	0.13		
Erosion rate (sqrt)	Intercept	$2.1*10^{-2}$ ($3.4*10^{-3}$)	<0.0001	**0.035**	0.48
	Density	$9.1*10^{-7}$ ($3.3*10^{-7}$)	**0.035**		

Figure 2: Pictures showing different density treatments before and after erosion. A: Control before erosion, B: Detail of control after erosion with visible erosion of thin sediment flakes, C: 4,000 ind./m² before erosion, D: Detail of 4,000 ind./m² after erosion with local erosion around the burrows, E: 20,000 ind./m² before erosion and F: Detail of 20,000 ind./m² after erosion with protruding burrows and visibly erododed sediment between the burrows.

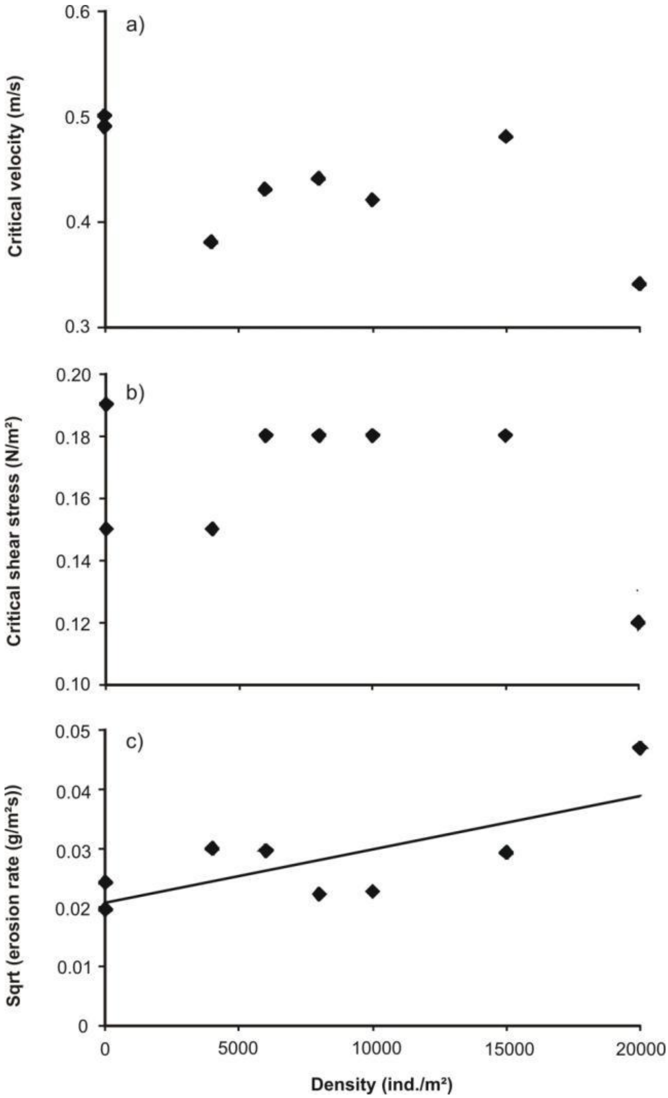

Figure 3: Critical average flow velocity (a), critical shear stress (τ_{crit}) (b) and square root transformed erosion suspension rate (c) for different densities of *Corophium volutator.*

The relationships between delta SSC (SSC dimished with SSC at the start of erosion) and the squared average flow velocity at the different *C. volutator* densities are illustrated in Figure 4. Slopes are significantly different between treatments (ANCOVA, $F_{7,\ 31}$ = 9.6, p<0.0005), and although not consistent, the general trend is that the suspended sediment concentration increases faster with average flow velocity for higher densities of *Corophium volutator*, once erosion has started. This indicates that a higher degree of bioturbation due to higher densities, increases the amount of sediment that is eroded. Especially for the treatment of 20,000 ind./m², larger amounts of sediment were eroded at lower flow velocities compared to the lower densities and the references (Fig. 4).

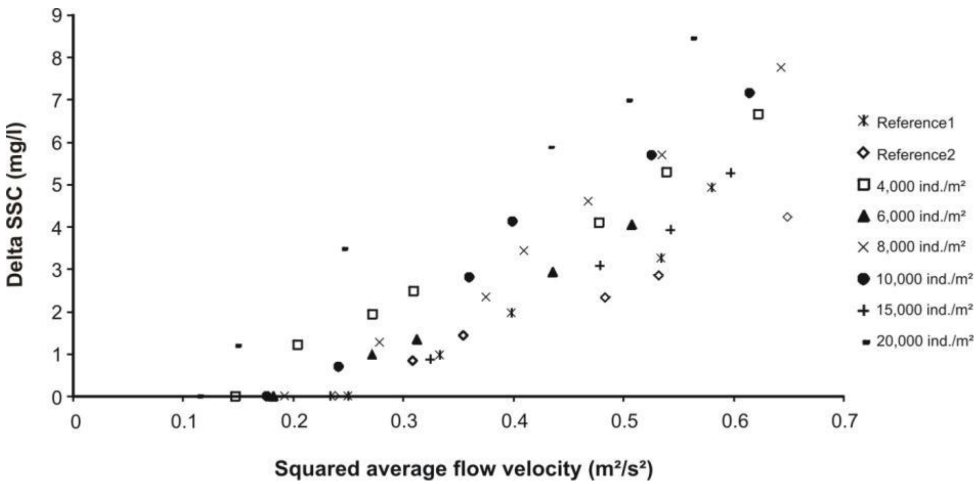

Figure 4: Relationship between suspended sediment increase (SSC, mg/l) and squared average flow velocity for varying densities of *Corophium volutator* after the onset of erosion.

4. Discussion

4.1. Considerations on flume experiments

Although it is the shear stress that controls the incipient motion of particles in flowing water (Léonard and Richard, 2004), the use of critical average flow velocity (Widdows *et al.*, 2000b; Ciutat *et al.*, 2007) can be justified, because in similar flow conditions in the same erosion flume, there exists a relation between average flow velocity and bed shear stress of the form $\tau_b = \mathrm{A}\overline{U}^2$, where A is a characteristic of the flume (Toorman and Luyckx, 1997). Until now, there exists no standardised experimental set-up or method to determine shear stress. Therefore, it is difficult to compare absolute values of shear stress between different studies, since differences in the experimental set-up and the determination of shear stress will give different absolute values (Tolhurst *et al.*, 2000; Adam, 2009). In our flume, turbulence measurements were preferred to bottom shear stress derived from the logarithmic profile, since the flume was too short to develop a logarithmic profile (Adam, 2009). Moreover, turbulence was easier and quicker measurable than a velocity profile. Reynolds stresses were neither measured, because these are highly sensitive to tilt and secondary currents (Adam, 2009; Kim *et al.*, 2000; Nezu and Nakagawa, 1993), which cannot be avoided in a narrow flume. Turbulence measurements at a certain depth rely on the assumption that the sampling volume of the ADV is located at the peak stress elevation, which was taken as 7-10% from the water depth. From Direct Numerical Simulation (DNS) data, it is known that the shear stress is not constant over the transition layer near the bottom, and that the peak stress elevation is very close to the bottom (~3% of the water depth for the present flume). However, as explained above, it was practically impossible to take measurements at this peak stress distance. Nevertheless, Adam (2009) concluded that turbulence measurements were reproducible and easiest to perform. Since the sediment bed is homogeneous and air bubbles are avoided by thorough mixing, the point ADV measurements can be assumed to be valid for the whole sediment bed.

4.2. Impact of *Corophium volutator* on erodability

Corophium has several mechanisms to influence sediment erodability. It is essentially a deposit feeder, and deposit feeders have the tendency to physically eject sediment into the overlying water column (Graf and Rosenberg, 1997). *Corophium* was previously observed to flush its burrows during submersion (De Backer *et al.*, 2010), and the same observation was made in this study. de Deckere *et al.* (2000) concluded that this active resuspension significantly affected the suspended sediment concentration (SSC) in the water column at low flow velocities (<0.2 m/s), and that the SSC increased with increasing density. Deposit feeders are also known to disrupt the cohesive sediment structure making the surface sediment more susceptible to erosion (Graf and Rosenberg, 1997). Disruption of the surface sediment structure by *Corophium* is mainly due to feeding (scraping) and crawling on the sediment surface, which loosens sediment particles, so they can be more easily eroded. In the presence of a biofilm, feeding might as well indirectly influence sediment stability by decreasing the sediment stability due to reduction of the stabilising diatoms (Daborn *et al.*, 1993; Gerdol and Hughes, 1994a; Chapter 6). However, no biofilm was added in this flume experiment to stabilise the sediment, since this could impede the interpretation of the density-erodability relationship. Hence, feeding activity was most probably reduced, which might result in lower bioturbation activity (Nogaro *et al.*, 2008). Furthermore, *Corophium* activities increase the surface water content (Gerdol and Hughes, 1994a; De Backer *et al.*, 2009), which is positively related to erosion rate (Fukuda and Lick, 1980; Aberle *et al.*, 2004). The burrows built by *Corophium* might also influence sediment erodability, since they increase bottom roughness on the one hand, and strengthen the sediment with mucus secretions on the other hand. The activities of *Corophium* mainly impact the surface layer, and as such they mainly influence fluff layer erosion, characterised by (passive) floc resuspension at low stresses (Type 1a erosion; Amos *et al.*, 1992). In this experiment, fluff layer erosion was not directly measured, since that occurs at low current velocities of ± 9 cm/s and 11-12 cm/s (de Deckere *et al.*, 2003; Widdows *et al.*, 2009), and our erosion experiments started at 11 cm/s. Therefore, we measured bed erosion in relation to different densities of *Corophium*. We are aware that replication of our density treatments would have been much more powerful, but due to time and logistic constraints, replication was not possible. Therefore, the results should be treated with caution and ideally, similar experiments should be repeated with replicated treatments. Nevertheless, we observed that the effect of *Corophium* was predominantly an increase in suspension erosion rate with increasing density, and not a change in erosion threshold (τ_{crit}). A similar relationship between erosion rate and density was observed for other deposit feeders such as *Macoma balthica* (Willows *et al.*, 1998), *Nereis diversicolor* (Fernandes *et al.*, 2007; Widdows *et al.*, 2009) and *Hydrobia ulvae* (Andersen *et al.*, 2002; Orvain *et al.*, 2006). de Deckere *et al.* (2003) had results consistent with ours for *Corophium*, although the density range was much smaller. The increase in erosion rate was mainly caused by an increase of bottom roughness due to the burrow structures of *Corophium*, but active resuspension due to flushing and passive resuspension due to disruption of the sediment structure probably also contributed slightly to the increase in suspended sediment. Initial erosion of the sediment between the burrows was most probably due to a combination of a local increase in shear stress between the burrows and the sediment being more susceptible to erosion because of *Corophium* bioturbation. This led to a surface with protruding burrows, which resisted erosion due to the strengthening with mucus (Meadows *et al.*, 1990). These protruding burrows caused a further local increase in shear stress (Eckmann and Nowell, 1984), and this resulted in scour around the burrows and increased suspended sediment concentration.

No relationship was found between critical shear stress and *Corophium* density. Several authors found a similar independence of τ_{crit} for macrobenthos density of different species (*Cerastodema edule* by Ciutat *et al.*, 2007; *Hydrobia ulvae* by Andersen *et al.*, 2002 and Orvain *et al.*, 2006; *Macoma balthica* by Willows *et al.*, 1998 and *Nereis diversicolor* by Widdows *et al.*, 2009). However, for a density of 20,000 ind./m^2, a large decrease in critical shear stress was observed, which could be explained by the increase in bottom roughness with increasing densities. At this density, the entire sediment surface was covered with burrows, which resulted in a surface covered with small elevations and pits (Fig. 1e), and this influences the bottom current. In contrast, at the lower densities, burrows were more aggregated in patches (often at the edges of the mesocosm) (Fig. 1c), and in between the sediment surface was smooth, resembling the control sediments. These aggregations of *Corophium* individuals are the result of natural behaviour because high density patches on the cm-scale are also observed in the field, especially in winter when densities are lower. This patchiness is caused by intraspecific interactions among *Corophium* individuals or possibly through active aggregation (Lawrie *et al.*, 2000). Our results for independence of τ_{crit} at densities lower than 15,000 ind./m^2 are consistent with de Deckere *et al.* (2003) and Grant and Daborn (1994) for *C. volutator.* However, to our knowledge no other flume studies measuring critical shear stresses were performed with densities higher than our density of 20,000 ind./m^2. So, it would be interesting to see if shear stress further decreases when density is further increased or if it increases. When the density of burrows is high enough, theoretically at 47,000 ind./m^2 according to Nowell and Church (1979), a skimming flow may develop. A 'skimming flow' occurs when the spacing between the roughness elements is equal to or less than the element height (Vogel, 1994), and it leads to a shift of the stress peak above the tube tips resulting in sediment stabilisation and sediment deposition (Friedrichs *et al.*, 2000), which might also decrease suspension erosion rate.

Whether erosion of the intertidal sediments inhabited by *Corophium volutator* will occur in the field, not only depends on sediment stability, but also on the hydraulic stresses present on the tidal flat. A hydrodynamic model for the IJzermonding (Giardino *et al.*, 2009) shows that maximum average flow velocities over the intertidal flats with *Corophium* are around 0.1-0.25 m/s (equivalent to a bed shear stress of 0.024 - 0.15 N/m^2) dependent on the location on the mudflat. This means that, according to our results (see Figure 2a), bed erosion will rarely occur under normal weather conditions, since erosion started only at 0.34-0.5 m/s (0.12 – 0.18 N/m^2) in our experiments. However, hydraulic stresses can be higher under storm conditions or on *Corophium* inhabited mudflats with a different morphology. For instance on the Heringplaat in the Dollard Estuary, a maximum flood current was measured of 0.4 m/s equivalent to a maximum shear stress of 0.3 N/m^2 (de Deckere, 2003), which could cause enhanced erosion in the presence of *Corophium* in the field. On the other hand, a study in the Westerschelde, showed that *Corophium* predominantly occurred at low current velocities upto 0.25 m/s (Ysebaert *et al.*, 2002b). The preference for low current velocities could, hence, be a matter of ensuring its own habitat because bed layer erosion could favour other competing species because sediment properties change. SSC was not measured at low flow velocities in this study but active resuspension by *Corophium,* especially at high densities, and fluff layer erosion may significantly contribute to resuspension of sediment in the water column (de Deckere *et al.*, 2000).

Although this paper is limited to a laboratory experiment to assess the influence of *Corophium* on sediment erodability, we believe that this kind of experiments are needed to include the complex effect of biota in sediment transport models. Firstly, the results of such flume experiments should be used to calibrate a model explaining the rate of erosion. E.g. Willows *et al.* (1998) modeled the increase in resuspension due to the bivalve, *Macoma balthica*, with 9 parameters, including the excess flow velocity above a critical flow velocity. Secondly, the model should be checked for its application in natural situations by performing field experiments with realistic flow conditions. A third step could be the inclusion of the model in sediment transport models which have enough spatial detail to include *Corophium* inhabited areas. Since our experiments show that *Corophium* enhances sediment erodability only if highly abundant, the decrease in critical shear stress for erosion and the increase in rate of suspension should only be included in simulations covering late spring and summer time when the *Corophium* densities are highest (Chapter 6). However, currently, sediment transport models are not accurate enough and can not run simulations with the high detail needed to include biotic effects.

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